

THE RESURRECTION OF A SPECIES; *MUHLENBERGIA STRAMINEA* (GRAMINEAE)

Charlotte G. Reeder & John R. Reeder

Herbarium (ARIZ), 113 Shantz Building, University of Arizona, Tucson, Arizona
85721 USA

ABSTRACT

Muhlenbergia straminea, described by Hitchcock (1913), was recognized as a distinct species until 1935 when he relegated it to synonymy under *M. virescens* (H.B.K.) Kunth, a disposition that has been followed by all subsequent authors. The present study, based on morphology, distribution, and time of flowering presents strong evidence for the recognition of *M. straminea* as a species distinct from *M. virescens*. Although quite unexpected, we believe it is highly significant that meiosis occurs in the anthers of *M. straminea* in the autumn preceding flowering the following spring.

KEY WORDS: Gramineae, *Muhlenbergia straminea*, *M. virescens*, *M. curvula*, *M. quadridentata*, México, southwestern U.S.A.

Continuing field and herbarium studies, along with examination of type specimens, have revealed the need to re-evaluate certain members of the *Muhlenbergia montana* complex. This group includes species most easily recognized by the 3-nerved (often 3-toothed and/or 3-awned) second glume and lower sheaths which become flat, somewhat papery, and no longer invest the culm. A number of species, most of which occur in México, make up this taxonomically puzzling assemblage of both annual and perennial grasses. Of immediate concern is the perennial *M. virescens*, a taxon said to range from Central México to Arizona and New Mexico, U.S.A. The species is based on *Podosaemum virescens* H.B.K. (1816), which was described from a plant collected by Humboldt & Bonpland in 1803 in the state of Guanajuato, México: "Crescit locis asperis, excelsis regni Mexicani prope Santa Rosa de la Sierra et Puerto de Varientos, alt. 1350 hexap. [ca. 2400 m]. Floret Septembr." The type specimen (P!) is fragmentary, consisting of a segment of culm with an inflorescence partially included in the upper sheath, another short section of culm with leaf attached, and a separate leaf. Written on the sheet is the locality, "S. Rosa." The description is quite ample, and along with the type specimen, gives an adequate conception of the species. Numerous specimens (including our own) collected in the mountains of Guanajuato can be determined as this species with little difficulty. The

transfer to *Muhlenbergia* was made by Trinius (1824), some five years before Kunth (1829) as cited by Hitchcock (1913, 1935, 1935a, 1951). Prior to 1913, Trinius was given as the authority for this transfer. It is noteworthy that Kunth (1833) recognized the Trinius combinations.

There has been, and continues to be, confusion regarding the range of *Muhlenbergia virescens*. Roemer & Schultes (1817), Hemsley (1885), and Fournier (1886) repeat the distribution as given in H.B.K. (1816), which suggests that the species is confined to Central México. Fournier often cited other collections but here listed only the type number. Hemsley's work, based largely on Fournier, included no additional information.

Meanwhile Scribner (1882) published a detailed list of grasses collected by C.G. Pringle in Arizona and California during the summer of 1881. Included (p. 88, 89) is: "32. *Muhlenbergia virescens*, Trin., *Unifl.*, 193; Kunth, *Enum. Pl.* i, 202, et *Suppl.* 160; *Podosaemum virescens*, H B K., *Nov. Gen.*, i, 132; *Trichochloa virescens*, R. & S., *Syst.*, ii, 389." One finds (p. 88, 89) a rather lengthy description of a plant collected on "Summits of the Santa Rita Mts., Arizona. . . . This species resembles *M. gracilis* Trin., in habit, but is distinguished at once by its very long involute leaves and light colored, more loosely flowered panicle." [*M. gracilis* sensu Amer. auct. is considered to be *M. montana* (Nutt.) Hitchc. True *M. gracilis* (H.B.K.) Trinius is not a synonym of *M. montana* but a related species.] Lastly this comment (p. 89): "This is a Mexican grass, not before observed in the distributed collections made within the limits of the United States, and perhaps now found for the first time within our limits. It should be added that identification of Pringle's specimens with *M. virescens* Trin., is based upon descriptions of that plant only."

This report by Scribner (1882) of the occurrence of *Muhlenbergia virescens* in the Southwestern United States appears to account for Vasey (1883, 1892), Beal (1896), and subsequent authors having added Arizona and New Mexico to its range. Vasey (1892) included a detailed description of *M. virescens* stating (p. 67): ". . . New Mexico, Arizona, and Mexico." Hitchcock (1913), in *Mexican Grasses*, indicated that the range of *M. virescens* extended from central México into New Mexico and Arizona. Two years later Wootton & Standley (1915), in their *Flora of New Mexico* cited (p. 72) "18. *Muhlenbergia virescens* (H.B.K.) Kunth" [obviously following Hitchcock 1913], quoting the type locality from H.B.K. The range is given as "Arizona and New Mexico to Mexico." There is no description; however two collections are cited: *Palmer* from northwestern New Mexico, and a *Bigelow* gathering from Ben More (sic!) [a peak near Santa Rita, in eastern Grant County]. A specimen (at US) collected by Edward Palmer *s.n.* [no date] gives only "State of New Mexico."

Hitchcock (1913, p. 301) listed *Muhlenbergia virescens* (H.B.K.) Kunth, *Rév. Gram.* 1:64. 1829. He indicated that it is based on *Podosaemum virescens* H.B.K., and quoted the type locality from the original description. The range, however, includes New Mexico and Arizona. Three collections from México are listed: *Rose* 3527 from Sierra Madre, Zacatecas, and two *Parry & Palmer* numbers (920 and 928 in 1878), both from San Luis Potosí.



Fig. 1. Habits and spikelet details. A, *Muhlenbergia virescens*, from Scribner (1897); B, *M. straminea*, from Hitchcock (1951).

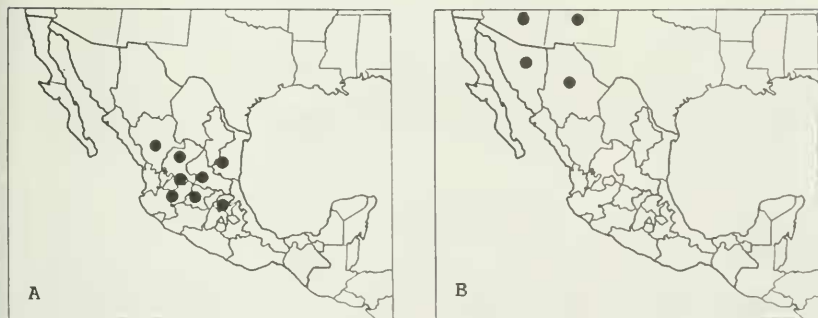


Fig. 2. Distributions of A, *Muhlenbergia virescens* and B, *M. straminea*.

TABLE I

Chromosome Numbers for *Muhlenbergia straminea* and *M. virescens* (All collections are Reeder & Reeder, with vouchers deposited at ARIZ.)

Muhlenbergia straminea

Collection	2n	Locality
6903	21	AZ: Cochise Co., Chiricahua Mts., Rustler's Park Campground. 2530 m 16 Oct. 1977.
6906	22	AZ: Pima Co., Santa Catalina Mts., near Loma Linda Picnic area. 2440 m 18 Oct. 1977.
6907	22	AZ: Pima Co., Santa Catalina Mts., above Geology View Point. 2165 m 18 Oct. 1977.
6908	20	AZ: Graham Co., Graham [Pinaleno] Mts., near Shannon Campground. 2774 m 19 Oct. 1977.
6909	21	AZ: Graham Co., Graham [Pinaleno] Mts., Turkey Flat. 2316 m 19 Oct. 1977.
6910	20	AZ: Cochise Co., Huachuca Mts., Carr Canyon. 2195 m 21 Oct. 1977.
6911	20	AZ: Cochise Co., Huachuca Mts., Carr Canyon. 2255 m 21 Oct. 1977.
6914	22, 24	NM: Grant Co., Cherry Creek Campground, N of Pinos Altos. 2103 m 26 Oct. 1977.
6918	20, 21	NM: Catron Co., S of Luna. 2440 m 27 Oct. 1977.
6922	20, 24	AZ: Navajo Co., N of Indian Pines. 2250 m 27 Oct. 1977.
6924	20	AZ: Coconino Co., San Francisco Mts., on Snow Bowl Road. 2440 m 28 Oct. 1977.
6926	20	AZ: Gila Co., along Old Mogollon Rim Road. 2225 m 28 Oct. 1977.
6928	20	AZ: Gila Co., along Old Mogollon Rim Road. 2440 m 3 Nov. 1977.
6929	20	AZ: Apache Co., SE of Big Lake Campground. 2680 m 4 Nov. 1977.

Muhlenbergia virescens

Collection	2n	Locality
4750	20	MEX: Guanajuato, 9.5 km NE of Ciudad Guanajuato. 2450 m. 19 Oct. 1966.
4751	20+1	MEX: Guanajuato, 27.5 km NE of Ciudad Guanajuato. 2400 m 19 Oct. 1966.
4965	40	MEX: San Luis Potosí, 19.5 km SW of Ciudad San Luis Potosí. 2250 m, 15 Sept. 1967.

TABLE II

Comparison of morphological features between *Muhlenbergia virescens*, *M. curvula*, and *M. straminea*.

	<i>M. virescens</i>	<i>M. curvula</i>	<i>M. straminea</i>
Basal sheaths and blades	straight	straight	curling, like wood shavings
Blades	involute	involute	flat, becoming involute at tip
Blade width	ca. 1.5 mm	ca. 1.5 mm	2.5--3.5 mm
Blade surface	scabrous below, hispid above	scabrous below, hispid above	scabrous below, with tiny spicules between the ribs above
Inflorescence color	green or dark green	dark green	yellowish or pale green
Glume I	(1.5) 2.0--3.0 (3.5) mm	(2.4) 2.5--3.0 mm	(3.0--3.5) 4.5--5.0 mm
Glume II	(3.0--3.5) 4.0--4.5 (5.0) mm	4.0--4.5 (5.0) mm	(4.0) 4.5--5.5 (6.0-7.0) mm
Glume surface	glabrous, shiny, translucent	glabrous, translucent	dull, minutely scaberulous
Lemma	(3.0) 3.5--4.0 mm	3.5--4.0 mm	4--5 (6) mm
Lemma surface	pubescent on lower 1/2--2/3	pubescent lower 2/3	pubescent on midrib at base and on margins on lower 1/2
Stamens	2.0--2.5 (3.0) mm	ca. 2 mm	(2.0) 2.5--3.0 mm
Flowering time	Sept.--Oct.	Sept.--Oct.	March--April (May)

Recent authors, e.g. McVaugh (1983), Beetle (1987), and Allred (1993) have continued to include the southwestern United States within the range of *Muhlenbergia virescens*. McVaugh (p. 263) states "Open dry grassy places in sparse oak or oak-pine forest, 1600--2700 m on the Central Plateau and the ranges to the west, flowering Oct--Nov." He includes "S w U.S." as well as various central and western states of México. Beetle (1987) cites "New Mexico and Arizona, south to Michoacán and Mexico." Allred (1993) gives only the distribution within New Mexico.

Hitchcock (1913, p. 302) described as new *Muhlenbergia straminea*, the type collection, R. Endlich 1210, 10 April, 1906, from pine and oak woods, Tecorichu, western Sierra Madre, Chihuahua, elev. 2200 m. Two other gatherings from the same general area are cited: Endlich 1226 and 1210a, from Tierra Colorada, dated April, 1906. [Hitchcock indicated that the specimens at US are from material sent him by Dr. I. Urban, Berlin Botanical Garden.] There is a rather lengthy description, followed by (p. 302): "This species is distinguished by the stramineous appearance of the glumes and foliage and by the flat, ribbon-like lower sheaths, which withdraw from the culms and become spirally twisted or curled like shavings. The long, papery glumes indicate an affinity with *Triniochloa* but it is distinguished from that genus by the terminal awn of the lemma. It appears to be most nearly allied to *M. longiglumis* [Vasey, G., Contrib. U.S. Natl. Herb. 1:283. 1893]."

Muhlenbergia straminea may somewhat resemble *Triniochloa*, however careful examination reveals that the members of the latter genus are characterized by closed sheaths, and lodicules which are often fused and lack vascular traces. Also the leaf anatomy is pooid; in *Muhlenbergia* it is eragrostoid (chloroid). *Triniochloa* is clearly related to *Melica* and *Schizachne*. [See J.R. Reeder Systematic position of the genus *Triniochloa* (Gramineae). Amer. J. Bot. 55:735. 1968 (abstract).]

Muhlenbergia longiglumis is an attractive Mexican species with compressed-keeled sheaths, and long glumes which may be aristate. Soderstrom (1967) included it as a member of § *Epicampes*. *Muhlenbergia straminea* belongs within the § *Podosaemum* as outlined by Soderstrom, and is related to the *M. montana* group of species. In fact when Hitchcock treated the genus in the North American Flora (1935a), he placed *M. straminea* as a synonym of *M. virescens*, but gave no reason for this change. Since the original material of *M. virescens* was collected in central México, and the type specimen of *M. straminea* came from the mountains of northern Chihuahua, it seemed prudent to re-examine these two taxa with respect to the plants which are to be found in Arizona and New Mexico.

Perhaps one of the most striking differences to be noted from the protologues of these taxa is that the original material of *Muhlenbergia virescens* was collected in September; that of *M. straminea* in early April. Anyone familiar with "*M. virescens*" in the mountains of New Mexico and Arizona is aware that it blooms very early in the spring. Another characteristic, perhaps known only to us, is that the flowers are actually initiated in late autumn, at which time meiosis in the microsporocytes occurs. We tried unsuccessfully for several years in early spring to collect young inflorescences for cytological examination. Even though panicles had not yet emerged from the sheath, the anthers were already fully formed and contained mature pollen grains. At this time also, anthers have their characteristic reddish purple color, which is retained in the fixative and in 70% alcohol in which they are stored. Eventually we discovered that good cytological material can be collected in late September to early

November. Numerous good chromosome counts were obtained from collections made in late autumn in various localities in Arizona and New Mexico. The possibility that meiosis might occur in the autumn of the previous year occurred to us when we found plants partially covered with snow in March, many of which had inflorescences exposed, some well exerted from their sheaths! In contrast, we have observed *M. virescens* in full flower from August to October, and at that time have collected young inflorescences in satisfactory condition for cytological examination. Although, as can be seen in Table I, collections for chromosome counts for both *M. virescens* and *M. straminea* were made in the month of October, there is an important difference with respect to the time involved for the completion of flowering. As mentioned above, the initiation of meiosis within the anthers of *M. straminea* takes place in late autumn, and the plants remain dormant during the winter, blooming in early spring of the following year. In the case of *M. virescens*, meiosis occurs in late summer or autumn, and the plants bloom soon after in the same season.

In 1951 little was known regarding the flowering habits of this southwestern grass. In Gould (1951), C. Reeder (p. 211) made the following comment: "... flowering March to June and occasionally again in the summer and fall. New Mexico and Arizona to central Mexico. An interesting forest bunchgrass, closely related to the widespread and variable *Muhlenbergia montana* complex but rather unique in its spring-flowering habit and conspicuous with its peculiarly coiled leaves [and sheaths] and strikingly colored anthers." Obviously the idea that it may flower in late summer or fall arose from the early emergence of next-year's panicles. ARIZ has at least one such specimen, *L.N. Goodding M-314* (ARIZ-55284) from the Huachuca Mts., Cochise Co., Arizona, 5 Nov 1937. It is worth noting that specimens of this southwestern species collected after late April ordinarily consist of empty glumes with few or no florets. Even at this stage, the plants can usually be identified by their characteristic glumes and curling foliage.

It is true that *Muhlenbergia virescens* and *M. straminea* share certain characteristics, e.g., both are commonly to be found in oak or pine-oak forests in the higher mountainous areas of México and southwestern USA (mostly between 1900 and 2800 m); a fragile hyaline ligule commonly 10 to 20 mm long; subequal long acute or acuminate glumes, the first 1-nerved, the second 3-nerved; and narrow somewhat contracted panicle. There are, however, a number of morphological differences which serve to distinguish these species even on herbarium sheets (Table II).

Swallen (1950) described as new *Muhlenbergia curvula*, which he appears to have compared to *M. virescens* based on the northern element (*M. straminea*). This is not surprising since the descriptions of *M. virescens* in North American Flora (1935a) and Hitchcock's *Manual* (1935, 1951), as well as the illustration in the latter work, are based on the northern plants. In the *Manual* the figure of this species (1935, fig. 785; 1951, fig. 566) is drawn from *Pabner 565* in 1890 collected at Willow Springs, Navajo Co., Arizona. The type specimen of *M. curvula* came from México: Guanajuato: "12 miles from [Cd.] Guanajuato on road to Santa Rosa," Sept. 30, 1946 *H.E. Moore Jr. 1353* (US-1963089!). Since the Moore specimen fits well within *M. virescens*, we consider *M. curvula* Swallen and *M. virescens* (H.B.K.) Trinius to be synonyms. Further justification for this change is the fact that the type collections of both species came from essentially the same area in Guanajuato, México.

Of particular interest is *Parry & Palmer* 920 in 1878 (US-995807) from San Luis Potosí area, México, elevation 6,000--8,000 ft., on which one finds in Mrs. Agnes Chase's script: "Like HBK type of *Pod. [Podosaemum] virescens*." This specimen does, indeed, resemble the type of the Humboldt & Bonpland collection (P!), but in no way resembles *M. virescens* as illustrated in Hitchcock's *Manual* (1935, 1951). (fig. 1,B). Scribner (1897, fig. 110, p. 128) in *American Grasses-Illustrated* has a sketch of *M. virescens* which is quite consistent with the type, although his comment below the figure gives: "At an altitude of 1800 to 2400 m on the mountains of Arizona and New Mexico. Mexico. May, June." (fig. 1,A). Although the figure fits our concept of *M. virescens*, the range given for the species includes *M. straminea*, but he has noted the early flowering of the southwestern material. In 1891 Vasey reported on grasses collected by Dr. Edward Palmer in western México and Arizona. On p. 114 one finds "*Muhlenbergia virescens* Trin." from "Near the summit of the mountain Alamos." March 26 to Apr. 8. 1890. US has four sheets of this number; all prove to be *Muhlenbergia straminea*. This species has been collected more recently from about the same locality in Sonora, México, by V.W. Steinman & M. Baker 9373 on March 11, 1993 (ARIZ). Other collections from the mountainous areas of Sonora and Chihuahua have appeared within recent years. For the distribution of these two species see Figure 2.

Of the new species recently described by Y. Herrera (1987, 1992) from México only one appears to pose any problem of separation from *Muhlenbergia straminea*. The type of *M. durangensis* came from Mpio. Mezquital, state of Durango, and like *M. straminea* flowers early in the spring. However, it may be distinguished by its very short truncate ligule (0.7--1.0 mm long) which has short acute projections from the sheath on either side. Further, the spikelets tend to be larger (5.0--6.5--7.0 mm long), and anthers mostly 3.0--3.5 mm long. The other species (*Muhlenbergia cualensis* and *M. michisensis*) differ in having only one nerve in the second glume. In both *Muhlenbergia virescens* and *M. straminea* the second glume is distinctly 3-nerved.

In a recent paper, Herrera & Grant (1993) consider the correlation of morphological and flavonoid data within the *Muhlenbergia montana* complex as generated by the DELTA system. The discussion does not instill great confidence, e.g. one finds the repetition of three separate collections under two different species. Further, the inclusion of *M. argentea* Vasey within this complex is puzzling. Even though Vasey (1886) in the original description of *M. argentea* stated that the upper "empty glume" is "three-toothed at the apex," Beal (1896, p. 232) described the glumes of *M. argentea* as "subequal, linear-lanceolate, the apex more or less 2-toothed, 1-nerved." Hitchcock (1935a, p. 465) described the same species in some detail, basing his description on the type material, which was all that was available at the time. The glumes are said to be "about equal, thin, oblong or somewhat notched, the midnerve extending into a mucro or short awn, the summit minutely pubescent or ciliate." The glumes in specimens of *M. argentea* we have examined fit this description. Whereas the second glume in *M. argentea* may be 3-toothed in some plants, other characteristics do not suggest a relationship with the *M. montana* complex. The sheaths invest the culms and are slightly compressed-keeled; the glumes are 1-nerved; the lemma is deeply bifid; and of special note is the fact that the caryopsis is conspicuously flattened. *Muhlenbergia argentea* clearly is not a member of the *M. montana* complex.

In summary, *Muhlenbergia straminea* Hitchc. is shown to be a species worthy of recognition, and is not conspecific with *M. virescens* (H.B.K.) Trinius. *Muhlenbergia curvula* Swallen is reduced to synonymy with *M. virescens*. To our knowledge, the occurrence of meiosis in *M. straminea* in late autumn, preceding flowering the following spring, is unique among members of the *M. montana* complex.

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Note: The chromosome number of *Reeder 4965* from San Luis Potosí was determined to be $2n = 40$. It is of interest that in this instance meiosis is somewhat irregular with 4 or 5 quadrivalents clearly visible, suggesting that it may be an autotetraploid.

A better understanding of specific features, and the separation of *Muhlenbergia straminea*, reveal that three of our collections for which chromosome counts were reported earlier as *M. virescens* in fact represent the closely related *M. quadridentata* (H.B.K.) Trinius. The specific collections are 4664 and 4475 from Durango (Reeder

1967) and 4703 from Zacatecas (Reeder 1968). *Muhlenbergia quadridentata* may be distinguished by its shorter ligule which tends to be firmer near the base, frequently with vascular traces evident; blades, which are flat becoming involute, are strongly ribbed with tiny spicules on the ribs; and glumes that are dull (scaberulous and may have a few hairs at the base).

A few reports of *Muhlenbergia virescens* in the literature need to be clarified as well. McVaugh (1983) cited Reeder & Reeder 6437 from Monte Escobida, Zacatecas, as *M. virescens*. Re-examination of the specimen reveals it to be *M. quadridentata*, the lemma of which is pubescent on the lower 1/2 to 2/3. This type of pubescence is the principal character used by H.B.K. (1816) to segregate *Podosaemum gracilis* H.B.K. There is little else to distinguish these plants from their close relative, *M. quadridentata*.

McDonald (1990) listed *Muhlenbergia virescens* in an enumeration of species from alpine-subalpine mountains of northeastern México. He indicated that the grasses were identified by us. Another check, along with the separation of *M. straminea* and *M. virescens*, shows that indeed McDonald 2045 from the Peña Nevada, Tamaulipas, is true *M. virescens*, whereas McDonald 2100 from Sierra La Vega, Coahuila, is *M. quadridentata*.